MORPHOLOGICAL INSTABILITY, ESPECIALLY IN PINUS RADIATA

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(WITH TWO FIGURES AND PLATE XIV)

The various behaviors of the vegetative and reproductive shoots in the Coniferae have for many years been the objects of extended observation and experiment, and these have been the basis of a massive literature. From this we may derive no mean conception of the amount of morphological instability which characterizes that genus which, in some regards at least, is the most highly specialized of all, namely *Pinus*. Of the conditions which discover such instability, injury has been the most efficient, the resulting unusual developments being said to be due to disturbed nutrition, especially over-nutrition. Precisely what is meant by this is not and cannot at present be stated, so that any light which experiment or the diversity of behavior in nature may afford us should be welcomed, especially if it may lead to a more specific indication of the most potent of the causes which must always be at play.

Evidence of such specific value is given us by the Monterey pine (*Pinus radiata*), a species as definitely restricted to a small area as the famous Monterey cypress (*Cupressus macrocarpa*), a geographical neighbor. The center of this area is, as nearly as may be, at Carmel-by-the-Sea, where is stationed a laboratory of the Carnegie Institution of Washington. The detailed descriptions of California trees in JEPSON'S *Silva of California* render minutiae unnecessary, though it may be noted in passing that among the teratological observations no mention is made in this work of the peculiarities to be noted below.

Carmel is situated in a forest of *Pinus radiata*, not, however, to the advantage of the tree. It is becoming more and more overcome by borers and fungi. It is, in any event, a short-lived tree of small dimensions but very rapid growth, a fact of importance in the present connection. It grows readily under cultivation, and

is very commonly seen in gardens, having either started by chance or by being planted. It is even used as a hedge plant, though of indifferent value for the purpose. But this circumstance leads often to the trimming of young trees, and so enables us to judge of the relative effect of traumatic stimulus as compared with another, namely, the amount of soil water, in producing unusual responses.

It must be prefaced that the amount of soil water in the normal habitat of this pine runs down very markedly during the long growing season, in spite of the moisture-laden atmosphere. Exact measurements are lacking, but the fact is sufficiently evident from the behavior of the vegetation in general, which becomes during the summer months of a distinctly xerophytic character. To this condition is due the gradual reduction in length of the fascicled leaves toward the apex of the season's growth, giving to the foliage of the leaders a cone-on-cone profile. PHILLIPS[1] has observed the same fact in *Pinus cembroides* Zucc., the Mexican piñon, in the mountains of southern Arizona, in a habitat which may, as regards soil moisture at any rate, be compared pretty closely with Carmel.

When grown in gardens, however, it generally happens that a greater abundance of water is provided, toward which a marked response is shown, both in amount of growth and in abnormal behavior. This is most obvious in an open spot used as an experimental garden within the grounds of the Carnegie Laboratory. Here the soil is kept abundantly supplied with water from springs, and here grows a cluster of young trees with heights ranging up to 30 feet or over. Aside from the generally well developed character of these, they all have fascicles which in the majority of cases proliferate. So numerous are the resulting short shoots that the branches become densely clothed, enough so as to quite hide the parent shoot itself from view when looked at from above.

Interest attaches to the phenomenon less because of the morphological fact, since it has long been known that pine fascicles do sometimes proliferate,[2] than because of their abundance and the

[1] Plant World **14**:66. 1911.

[2] For the literature on this see THOMSON, R. B., The spur shoots of the pines (to appear in the next issue of this journal), the manuscript of which the author has kindly allowed me to see.

regularity and constancy of their production. They appear, not, as might be expected, when the fascicles are young, but in those three or four years old especially. Unlike the lateral shoots of the whorls of branches, they are always negatively geotropic. This feature is brought out sharply in pl. XIV, *B*, which shows a length of a three-year old branch between whorls. The fact that fascicles as old as three or four years can renew their youth is worth notice. Those of *Pinus Taeda* in Alabama have been found to proliferate after two years, having been stimulated to grow from injury by cattle. This was in the cases of a couple of small trees which were six or eight years old. So far as I have been able to observe, in no instances do the abnormally developed spur shoots become permanent branches in *Pinus radiata*, although that there is evidently nothing in their nature to prevent further development appears from the fact that such is the case in *Pinus Taeda* (fig. 2, *B*). I have thought that the rapid rate of growth of the parent branch and the smallness of the spur shoots rendered successful histological articulation difficult, discrepancies which would be reduced if the parent branch is small to begin with, and of not rapid growth, as is true of *P. Taeda*.

Another example, and a still more striking one, I found at Carmel in the yard of Mr. SLEVIN, who kindly made a photograph for me. Except below, it was entirely without whorls, though a few extra-verticillate but ill-developed branches had grown. This abortion of whorls is quite common in this tree, but has been seen in other Coniferae (PHILLIPS, *loc. cit.*). The tree was growing quite near a cesspool. As the photograph shows, the whole of the chief stem (save for a small stretch) was densely clothed with foliage, due to the proliferation of nearly every fascicle, so that a fox-tail effect was produced. In the lower part of the stem, at the level of the bottom of the photograph, the spur shoots were dying and dropping off. Above they were growing, and the longest had attained a length of several centimeters. It was evident, however, that they were not able to become permanent in character, and there was no evidence that any of the branches had originated from fascicles.

I found no other such examples. Occasionally in small trees

which had been trimmed I saw a tendency for the fascicles to proliferate, but it was quite evident that pruning is by no means as efficient a factor as water supply. At the same time, we are bound to note that precisely where such a supply is abundant, and, in a remarkable case shown in fig. 1, where nitrogen in some form must have been quite plentiful, the development of verticillate branches was arrested. Other cases of absence of whorls were noted at Carmel, but only in gardens, though we know them to occur in nature

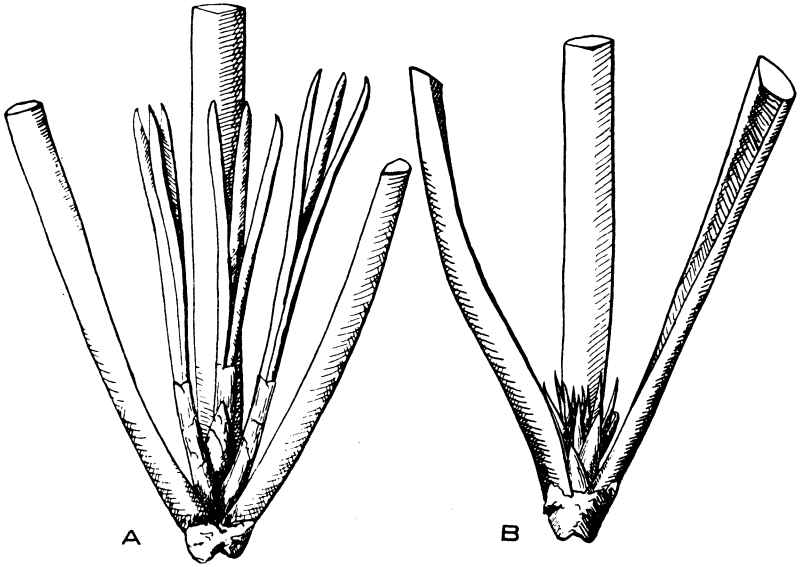


FIG. 1.—Proliferated spur shoots of *Pinus radiata: A*, the shoot so formed produced fascicles at once from the axils of the fascicled leaves of the spur shoot; *B*, hypertrophied scale leaves produced on the proliferating axis.

in other species. It is evident, however, that it is not due to less favorable soil conditions even here, since PHILLIPS (*loc. cit.*) notes that arrest of whorl development occurred in *Abies* on moist, rich sites in Arizona. One may conceive, furthermore, that a very rapid and energetic development of a chief shoot, especially in one in which the lateral shoots are not even laid down during the earlier part of period of growth, might be held responsible for failure to produce the usually formed lateral shoots.

Analogy in support of this view is not wanting, in general support of which may be cited also the apparently rather ready production of proliferations from spur shoots, with or without injury, in pine seedlings found by THOMSON. These seedlings grew in nurseries, probably under unusually favorable conditions for this

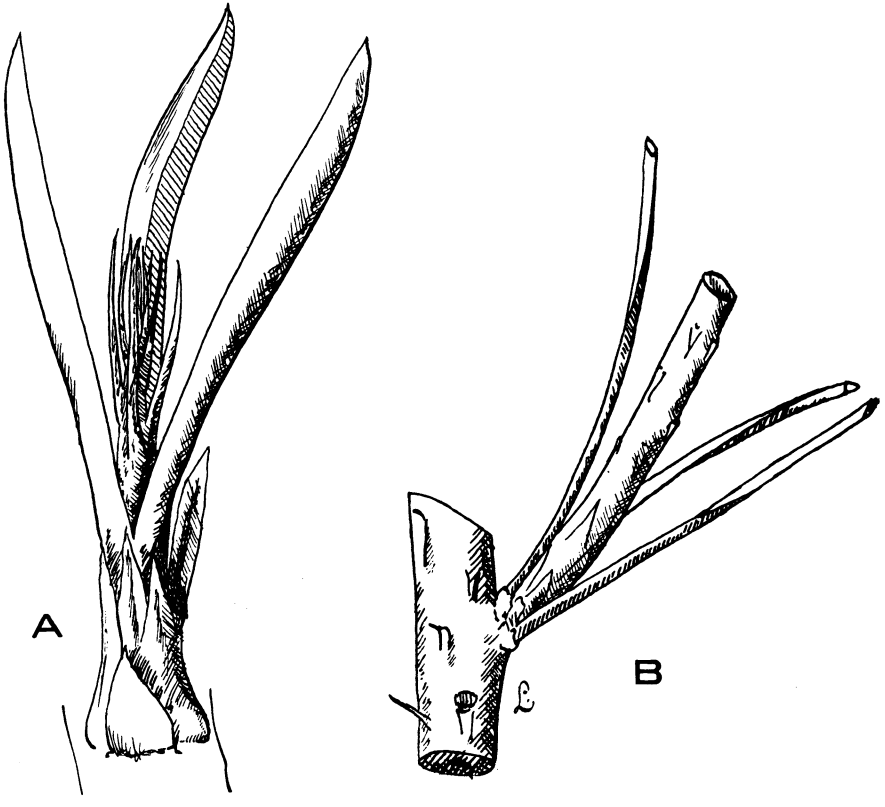
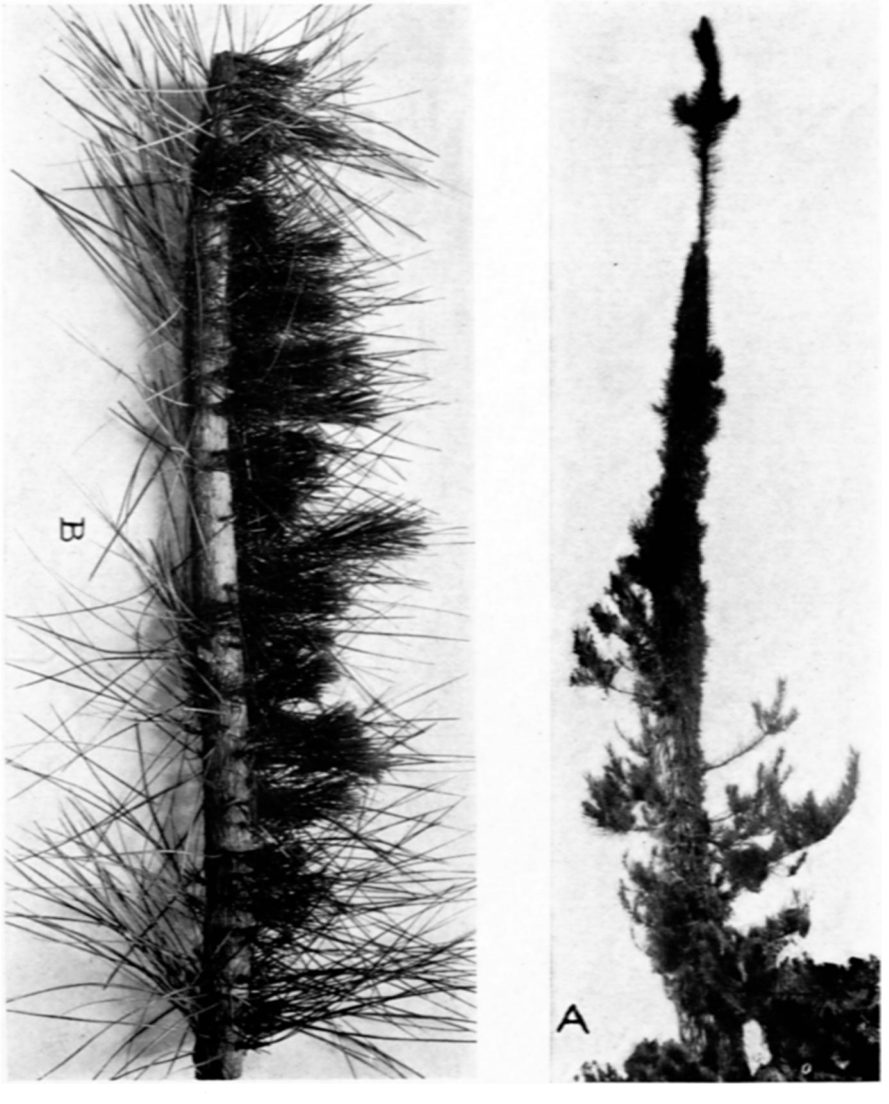


FIG. 2.—Proliferated spur shoots of *Pinus Taeda:* *A*, development of the axis below the whorl of fascicled leaves; *B*, a permanent branch formed by proliferation.

reason, especially as regards water supply. The likelihood that the spur shoots of mature trees do not proliferate, or if so more rarely than those of young trees or seedlings, is little lessened by my observations of *Pinus radiata*, since the trees were all young, or at any rate were not mature.



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The character of the shoot produced by proliferation of the fascicular bud is worth further notice. As seen by the text figures, the leaves succeeding immediately on the fascicled leaves may be either true scale leaves (fig. 2, *A* and *B*), or the same hypertrophied (fig. 1, *B*), and hence of juvenile character; or again, new fascicles may be produced at once in the axils of the three leaves of the parent fascicle (fig. 1, *A*), thus showing that fascicled leaves may subtend axillary buds. Far more rare than any of the preceding is the elongation of the axis of the spur shoot below the fascicled leaves instead of that above, as I found to occur in *P. Taeda* after injury. In such cases the leaves of the fasciculate whorl (fig. 2, *A*) do not attain their normal shape and dimensions, but are wider at the base and taper somewhat toward the apex, thus approaching hypertrophied scale leaves in form. Here, therefore, we have arrested fasciculate leaves and over-developed scale leaves approaching a common type, which probably simulates the form of the scattered leaves of the progenitors of the pines.

From the point of view of comparative morphology, it seems logical and in accordance with the facts to argue with THOMSON that the type of fasciculation seen in *Pinus* is a highly specialized condition, derived from a prototype in which the spur shoots are not limited in growth. As THOMSON, however, has taken up this question in the paper referred to, I leave it here. The degree of physiological plasticity displayed by various species of the genus, and especially the amount shown by particular ones, notably *Pinus radiata*, argues, in my own mind, for a comparatively recent origin of the kind of spur shoot characterizing it. The evidence above cited appears to favor the view that abundance of water is of prime importance in disturbing the ordinary equilibrium, and thus stimulating the proliferation of spur shoots.

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EXPLANATION OF PLATE XIV

A, small tree of *Pinus radiata* from which are absent the normal whorls of branches; the dense fox-tail effect is due to very numerous proliferated spur shoots; *B*, piece of a branch of another tree of the same species, showing the numerous proliferating spur shoots.